

# A HALF CENTURY OF PLANT PHYSIOLOGY<sup>1</sup>

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As has been clearly shown by the preceding essays important work had been done in the mechanics of plant life two centuries before the time of Sachs. He was therefore not the founder of the subject. His activities, however, have exerted a more profound influence on the study of life in plants than those of any worker in the subject and started physiology on a wholly unpredictable development.

The character of laboratory texts, lectures, instruction and research in the dynamics of plant life for the last half century was determined by the experimental investigations and theoretical conceptions developed by Sachs and the group of able workers who participated in the activities of his laboratories. When it is recalled that the list included Baranetzky, Bower, Brefeld, Francis Darwin, Detlefsen, Elfving, W. Gardiner, Godlewski, Goebel, Hansen, Hauptfleisch, Gregor Kraus, Klebs, J. Loeb, Millardet, H. Müller-Thurgau, Moll, Noll, Pedersen, Pfeffer, Prantl, Reinke, D. H. Scott, Stahl, Vines, deVries, Marshall-Ward, Weber, Wortmann, and Zimmermann, nothing more need be said as to his dominating influence on the development of the subject.

Naturally these men, as leading figures in the last decades of the century and the beginning of this, continued work begun with his advice and direction. The literature of the eighties and nineties shows that repetitious tests of the earlier results with extensions and refinements in experimental procedure absorbed a large share of the energies of workers in the laboratories of Central Europe, Great Britain, and America during this period. Work on sensitive tendrils, tropisms, and curvatures, and etiolation, may be cited as illustrations.

Sprouting, germination, and growth in its widest sense came in for great attention, especially since these activities were

<sup>1</sup> A paper read at the celebration held at the Missouri Botanical Garden, December 27, 1931, in honor of the one-hundredth anniversary of the birth of Julius Sachs.



made the criteria of so many tests of nutritive or environic factors. The conception evolved by Sachs of a specific formative material necessary to growth ran its course of usefulness until supplanted by modern studies of accessory substances and regeneration. That many of the findings of Sachs were modified or reversed by the results of more detailed experiments and with improved apparatus and advanced knowledge in no wise detracts from the enduring value of his achievements.

The most valuable feature of the Sachsonian contributions was that they set up no falsely appearing dead ends. Down a hundred corridors one might sense doors opening to new vistas. Immediately after Sachs the mechanics of cell-action and the visible features of structure and architecture of protoplasm were followed to the limit of microscopic vision. It soon became evident that the nature of protoplasm was not to be apprehended on the basis of spongy, emulsoid, or foamy structures revealed by the direct-vision microscope. Nearer approach to the essential and characteristic features of living matter was to be made only by studies in the realm of the ultra-microscopic, in which the theoretical conceptions of the colloidal physicist were relied upon to furnish a picture of the molecular meshwork.

The realization of the polyphasic nature of protoplasm has prepared us for the acceptance of the conclusion that the ultra-microscopic and filter-passing viruses are in fact ultimate centers of transformations of energy ordinarily attributed to living things.

Protoplasm was earlier supposed to consist of a mixture of proteins, but biochemical researches have made clear the presence of lipoids in the plasmatic mass and their importance as a colloidal component as well as the part they may play in energy-transformations.

Microdissection has now begun to play an important part in the study of essential characters of chromosomes and other bodies as well as of the plasmatic mass. The earlier conception of the cell-wall as a stratified cellulose formation has been gradually modified until at the present time it is realized that its constitution is determined by the protoplast with which it is intimately and actively connected, so that the expression non-living wall may not be correctly applied to any cell with surviving plasmatic material.



If it became necessary, however, to designate the single conception which has played the greatest part in the development of physiology in the last half century, the choice would undoubtedly be that of electrolytic dissociation and its concomitants. While the actual origin of this conception cannot be given, its formulation in a manner making it available to the physiologist was by Arrhenius in the eighties. With Pfeffer's results in osmosis and DeVries' determinations of isotonic coefficients it constitutes the basis of modern plant dynamics.

The ion or charged particle is now the unit to be considered whether mobilities, interferences, and antagonisms of elements are to be studied in turgidity, permeability, and in nutrition, or whether the electro-kinetic potential of the molecular meshwork of protoplasm is being considered in the connection with hydration and growth.

This paper would be extended far beyond its desirable limits in any attempt to describe the modifications of ideas of plant nutrition in experimentation and in agriculture which have resulted from studies in this field.

Perhaps the earliest effectual co-operation of chemists in the physiological field was that which came in the study of the enzymes. Some of these substances were known in the time of Sachs. Later contributions have consisted in finding a large number of these organic catalysts and in delimiting their specific action, as well as the range of their activity with respect to concentration of the medium, the accumulation of their products, and their relations to temperature. The proteinaceous character of the enzymes has led some writers to consider them as living matter. Some enzymes are known to carry a mineral element in their molecular mesh-work. It is to be recalled here that in addition to these complex bodies simpler catalysts such as some of the mineral elements have become known.

The study of the effects of radiant energy has been extended to observations of great delicacy in phototropism. It is a singular fact that when the philosophic definition of consciousness that makes this state depend upon modification of one irrito-motile reaction by another is applied to plants we do have activities that are, academically speaking, conscious. I refer particularly



to the case where an upright flower stalk in its development reaches a stage where it changes its position from the erect to the horizontal in response to gravity: it does so by a curvature in a direction determined by the impinging light.

Outside of this the basic unity of living matter yields no support for Aristotle's notion of an ascending complexity of living matter from the simplest plants to man. Plants and animals represent the two main surviving streams of living things in which only the inseparable colloidal characters of their living matter are the basis of comparison.

The fact that the organisms are so widely apart in their forms and modes of living calls for dissimilar perceptive mechanisms and transmission of stimuli. The wholly mystic nervous mechanisms and pulsations of Bose have so far eluded all observation, and nothing in the implied conceptions may be properly included within the domain of science, or of reality, or may be deemed worthy of metaphysical consideration.

It is of interest to recall that Sachs, commenting on the futility of the type of explanation in question, said: "We have no necessity to refer to the physiology of nerves in order to obtain greater clearness as to the phenomena of irritability in plants; it will perhaps, on the contrary, eventually result that we shall obtain from the process of irritability in plants data for the explanation of the physiology of nerves, and this, although it is yet a distant hope, gives a special attraction to the study of the irritable phenomena of plants."

Progress in the elucidation of the physical processes of transmission of nervous impulses in animals has, however, gone much farther than our understanding of homologous phenomena in plants. There is much sound evidence of effects being carried some distance by discrete particles or hormones, while in other cases the view that impulses may consist in disturbances of the electro-kinetic balance is favored. The study of the effects of interrupted action of stimulatory, regulatory, excitatory agents on "sensitive" organs has yielded some results which take on added value when compared with reactions in animals.

The study of the effects of duration, intensity, as well as wavelength, in photosynthesis is yielding some valuable results, while



the direct action of radiation in the region of the ultra violet and beyond on living matter is now known to be a matter of great importance in heredity as well as in growth and development.

The most prominent of the basic conceptions of plant physiology which have become the foundation of separate branches of science was that embodied in de Vries' mutation theory of evolutionary procedure. That differentiations in a line of descent should be by measurable units is a theoretical conception essentially physiological, matured in the mind of de Vries who had already contributed studies of electrolytic dissociation and its physiological implications.

It may be recalled that the evolutionary point of view received its earlier support from experimental evidence obtained by Charles Darwin in supplementation of his voluminous observations.

Following his pronouncements a vast literature of polemical writing appeared in which biologists and philosophers endeavored to express to the world what they thought of natural selection and of all other opinions on the subject.

The futility of mere discussion became apparent when de Vries, the experimental physiologist, entered the field presenting some new conceptions based on well-guarded cultures.

Phylogeny, evolution, and heredity were so vivified that researches were started in a hundred laboratories, and a dozen new journals are necessary for the publication of results.

It may be said that Weissmann's conception of germ plasm as the carrier of hereditary traits, invincible, inviolate and unmodifiable by environic causes, still holds, but only as conventional expression of the inertia of a strain of descent. Recent results, especially those obtained by subjecting organisms to the action of radiant energy of unaccustomed intensity or wave frequency, may destroy genes and alter linkages of characters causing breaks in transmission of hereditary characters of the most serious kind.

Practically all of the development of the study of bacterial organisms has been of a physiological character. The pathological action of these organisms on animals and man and crop plants has resulted in a development of this work into a separate branch with its own literature and laboratories, especially in pathology, in which fungi are also dealt with.



The separation has not gone so far, however, as to free the physiologist from his burden of understanding the action of soil bacteria and of fungi co-operating with the roots of higher plants in mycorrhizal arrangements.

Physiology has gone afield and quite literally in another manner in ecology. The study of organisms in a state of nature has been taken up by methods wholly new or materially modified from those which have been perfected in the laboratory. Physiology has thus been extended from the sea and the lakes, through swamps, fields, orchards, woods, plains and deserts to the mountain tops, with a development of many generalizations of the first rank.

Researches on the water-relations of plants have been widely extended in measuring transpiration, in the evaluation of the internal conditions and external agencies affecting the rate and amount. Attention directed to soil moisture and its use by the plant has resulted in a maze of literature of enormous volume. The wealth of facts recorded concerns almost all cultures, experimental or practical. The rate of loss, as well as the degree of hydration of the protoplasmic meshwork, affects almost all phases of metabolism and transformations of energy in the plant.

It is on the basis of these relations that water-loss is now taken to have been a prime factor in the evolutionary development of the higher plants, the ultimate expression of which is to be seen in the spinose and succulent forms of deserts.

The matter of the upward movement of sap has the distinction of a literature in which the essential problems were recognized two hundred and fifty years ago in the communications of Nehemiah Grew and of Malpighi to the Royal Society of London (1681). A little over two centuries ago (1727) Stephen Hales contributed notably to the subject, following which no contribution of enduring value was made until after the time of Sachs, although he and his co-workers and followers brought out a multitude of facts and a variety of explanations. The next notable advance was reported to the Royal Society in London by Dixon and Joly in 1895, this being the beginning of the development of the cohesion theory of the hydrostatic system of higher plants. The meshwork of water extending continuously from the



soil solutions wetting the root-hairs through the walls and lumina of vessels, tracheids, the colloidal masses of living cells in leaves terminating in ultra-microscopic menisci in the walls exposed to ventilated air spaces in the leaves, is the physical basis of this mechanism. The tensions set up by deformations in these surfaces may be as great as 200 atmospheres, and this pull is exerted on a meshwork of watery filaments capable of sustaining a stress of 300 pounds to the square inch. The configuration of this network or the path of sap varies widely with the morphology of the stems.

It is only since the time of Sachs that the transport of material from leaves or photosynthetic organs through petioles and stems to developing organs has been taken up seriously. No definite agreements have been reached as to the conduits, or the forces which are engaged. No comprehensive proposals have yet been made which can be taken as adequate to account for the amount and velocity of movement of the sugars, generally downward in the stem, although this subject has received the serious attention of some very able experimenters.

The amount and rate of upward flow of sap require the units of energy noted above, but it is also to be noted that the electrokinetic potential shows a gradient oriented to promote the flow in the xylem toward the apex of stems. Whether a reverse gradient found in the cortical region might be of importance in the movement of carbohydrates toward the base of the plant is a matter yet to be determined. The origin and nature of the so-called "root-pressure" is also undetermined after more than two centuries of observations and experiments.

The increases which are considered as growth in the broadest sense, the study of which received so much attention in Sachs' laboratory, have been for the most part dealt with by external measurements of one or two dimensions of organs, by total weight of individuals, by dry weight, or by counts of unicellular organisms. The approach is organogenic in any case. Studies of this character are essentially biographical, following the development of an individual or an organ from egg, parent cell or initial part way or on to maturity.

Earlier, the results were expressed in graphs showing the course



of growth plotted as velocities. During the last twenty-five years various efforts have been made to put the results into mathematical formulae. The rate of increase has been expressed in terms of the initial dry weight, and as compound interest on the initial dry weight.

Another view is that growth of an organ or individual may be given in the formula of an auto-catalytic reaction in which substance continuously secreted by the plant is the catalyst. The possibility of the identification of such a theoretical catalyst with the substance promoting fluidity or extensibility of the cell-walls is now meeting with some approval.

The analytical approach to the matter of growth is essentially that of Sachs who considered that division, elongation and differentiation are the stages from generative cells to permanent tissue. These three steps may now be characterized more closely as to the physical action involved.

During the first part of the existence of a new protoplast the dominant action is one of condensation of proteins and lipoids in a field near the iso-electric point nearly neutral or even slightly alkaline. The difference in this feature of the nucleus and of the cytoplasm is very slight. The entire protoplast has a low coefficient of hydration and permeability. Numerous very minute vacuoles are present which seem to have no connection with those that cause distention in the following stage.

With the attainment of full size, and seemingly consequent upon the movement of the chondriosomes from the neighborhood of the nucleus toward the periphery of the mass, a hysteresis or accumulation of solutions in vacuoles takes place. The osmotic action of these solutions which may have a value of 75 or 80 atmospheres is now the distentive agency which may enlarge the cell to as much as a thousand times its initial volume at a rate presumably regulated by the special catalyst present. The amount of protoplasm remains but little changed; dry weight of walls and other solids increase greatly.

Some proteins are broken up and some mucilages are formed. Granular bodies appear in the cytoplasm and the cellulose wall is formed. The H ion concentration increases in both nucleus and cytoplasm, but most in the external layers so that in a dis-



tended parenchymatous cell the nucleus may show pH 5.5, and the outer part of the cell pH 4 to 4.5.

Whatever validity the equations of growth calculated on dry weight or volume supporting the auto-catalytic nature of growth may have will depend on their correct expression of the formation and action of the accessory substance which increases the extensibility of walls in the distending stage, as the change in volume in the initial stage and in the final differentiation forms a very low proportion of the total increase in volume.

Differentiation may be least in parenchymatous cells, or it may be carried to the extreme limits known to the anatomist, with the progressive consumption or wastage of the protoplast. The final disappearance of living matter from a cell leaves it in a condition where only mechanical uses are served, such as rigidity, or as conduits of solutions or gases.

The theory of Sachs as to specific organ-forming substances has been gradually modified, so that now it is taken for granted that construction is at the expense of general food-material, forming proteins and lipoids at first and carbohydrates later. His idea is now replaced by the conception of regulatory agents facilitating distention by increasing the fluidity or plasticity of cell-walls. There is also good evidence of the action of substances which retard growth by influencing condensation or distention.

Two major modifications of our conception of living matter have been made in the last two decades in addition to those disclosed in the studies of the mechanism of heredity. One is to the effect that protoplasmic units, such as those in meristematic layers, display no inherent rhythms except as enforced by variations in the environment. Thus no periodicities have been discernible in the cultures of cell-masses from embryo chicks by Carrel, which have been carried along for nearly two decades.

Likewise we know that growing points and sheets of cambium show no regularly recurring variations of their own. The variations displayed are all resultant from seasonal changes, maturation of permanent tissues, the depletion or repletion of the available food-supply, loss or cessation of function of such organs as leaves. In other words, periodicity in plants complies with the seasons or is organogenic, but not protoplasmic.



Our generalizations as to the inertia of protoplasm have also been modified by observations as to the durability of the delicately balanced mechanism of living material. It is now known that protoplasts may live for centuries. This is quite aside from scholastic discussions as to the immortality of primitive organisms in which death of the individual is replaced by its division into two others which, with their descendants, undergo scission instead of death.

In our own laboratories we have identified not only parenchymatous cells, but also other elements, such as wood-fibers, well on their way toward mature differentiation, in which the protoplasmic bodies retain an effective organization through several centuries. In some of the solid bodies there is fair certainty that the actual molecular meshwork has continuously existed without replacement. Buried seeds have shown similar longevity, and it is highly probable that these structures could be prepared to survive tens of centuries with their low rate of metabolism.

Progress in the study of the energetics of the green plant as pertaining to chlorophyll action and to the energy-releasing reactions under respiration may not adequately be described in a brief discussion. Since the discovery of respiration by green plants by Ingenhousz in 1774, and Rollo's detection of the excretion of carbon dioxide by plants in the absence of free oxygen, in what later was termed intra-molecular respiration, research has been directed to the identification of the substances which were subject to oxidation, and of the products. The first attempt at standardization in this field was in the determination of the oxygen-carbon dioxide quantitative relation or respiratory quotient. This has been found to be affected by a wide variety of agencies. The excretion of oxygen by green plants in light, discovered by Priestley in 1772, may be taken as the initial observation of photosynthesis, but the subject was not given its modern form until the time of Sachs. It seems to be agreed that Sachs is to be credited with the realization of the action of the chloroplasts, and that chlorophyll was formed only in the presence of light.

The last half century of research has included many attempts to identify the primary processes and products in respiration, and



photosynthesis. In neither field have there been achieved decisive results, although a great volume of information has been accumulated which may be expected to fall into place when a comprehensive theory of the implied activities is propounded.

The effort is now being made to determine the unit of radiant energy necessary to produce a certain effect in this process, which might become a general standard of measurement of energy exchange or transformation in the plant.

With the earlier development of methods, physiologists, in striving for precision, fell into the grave error of an extreme concentration on specific effects. Thus, for example, a certain intensity of illumination, a certain temperature, or some concentration of a mineral salt was supposed to have an unvarying effect; and this was sought in the praiseworthy urge for standardization. It has dawned but slowly on the physiologist that the causative action of any one agency is conditioned by the intensities of all other forces acting on the organism. All of these have a range from zero to an endurable maximum, and any one of them may become a "limiting factor" in a process or in an organogenic development.

Physiology attracted researchers of ability in Europe from the time of Sachs. Its recognition as a phase of botanical science in America came two decades later in America. Dr. J. C. Arthur appointed to the chair of plant pathology and physiology at Purdue University, and myself, appointed as assistant professor of botany in charge of plant physiology at the University of Minnesota in 1893, seem to have held the first research and teaching positions, although the subject was being presented in a few botanical departments elsewhere.

That the subject included the processes basic to agriculture dawned but slowly even in the most advanced agricultural colleges. Here it may be in charge of members of the staff holding the most diverse titles. Its contributions appear in a great number of journals of a range far beyond the direct interests of biological science.

The opportunities for research and the facilities for teaching have grown in pace commensurate with those in cognate sciences. Chairs, departments, and laboratories are numerous: some are well equipped.



The requirements of a laboratory which gives instruction and advanced work and offers opportunities for research are much greater than for a department of animal—often termed general—physiology. Instruments of precision, specially designed optical, physical, and chemical apparatus, chambers and glass houses, a stock of growing material and a garden of some sort, are among the indispensables as contrasted with the window-ledge experiments with lamp-chimneys, remodeled alarm clocks, tinware, and kitchen appliances of forty years ago.

Not the least important feature of my subject is that of the change in the relations of the experimental scientist to his fellow man and to society in the period under discussion. At its beginning "pure science" really meant "sterile learning," devoid of human interest. The world at large was not interested in the results gained in technical laboratories, which achieved publicity only when they seemed, to the lay mind, blasphemous, or as trespassing on the "secrets of nature."

The scientist reacted to such a set of environmental conditions with an attitude of disinterest in the practical implications of his findings. Science and life were utterly apart.

The contrast with to-day is worth a moment's consideration. Some of you will present results at New Orleans which will appear in newspapers with a million readers within the week and may perhaps be put on the cables for foreign readers. This ready recognition may come for a new theory on some phase of protoplasmic activity, or for methods of using known facts for the benefit of the race.

Increased appreciation of the importance of our studies calls for a full sense of our responsibilities. The interests of the plant physiologist run back to that early stage of living matter when chlorophyll, or other sun-screens, was first developed. The problems of life he seeks to solve are those which began to crowd the stage of the world consequent upon this direct utilization of the sun's energy: they concern the existence and continuation of the entire organic world.

The technology of any worker who may contribute to knowledge in this great field must be stark, precise, and as free of mysticism as of sentimentalism. He has no magic carpet, but



falls into the chasms encountered unless he succeeds in bridging them or passing on temporary or "false" work.

Vitalism is to him the ready recourse of baffled minds, unequal to the relentless demands of sound experimentation. That there may be forms of energy releases in living matter not yet recognizable, which, like the ultra-Plutonian planets, disturb calculations of the protoplasmic system, is admitted.

To our contemporaries, however, the physiologist has come to be known as a worker deeply immersed in a bewildering maze of phenomena. His entire attention is given to compilation of refined methods and systemization of results, with but little attempt at realization of the broader philosophical aspects of his subjects.

Plant physiology has developed a sound methodology for the study of living matter, its involutions, properties, performances in functions, organogenesis, heredity, and evolutionary development. It has for this half century drawn upon chemistry and physics in perfecting a technique which has been extended with great profit in genetics, bacteriology, and ecology. The utilization of its methods has been of incalculable advantage in agriculture and the plant industries.

Researchers in physiology have been regrettably content with the vast array of material facts secured by experimentation and have not carried their work toward a realization of the first principles or abstract possibilities of living matter and of the broader aspects of the organic world. Research is most worth while when it is a search for explanatory knowledge.

Philosophical considerations which look toward analytical explanations are as truly ours to use as our laboratory equipment. The restricted conclusions based on tests and measurements may have but small importance in comparison with a metaphysical aspect of the possibilities. The constructive value of a contribution is not to be determined by the mass of facts presented, not by the bricks and mortar, steel and concrete it furnishes, but by the architectural conceptions which may be realized by the use of these materials.